Effects of forest litter on mycorrhiza development and growth of Douglas-fir and western red cedar seedlings

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Preparation of forest regeneration sites prior to conifer planting often includes slash burning or physical removal of soil organic matter. Experiments were conducted to determine if organic matter contributes to the mycorrhizal fungus inoculum potential in forest soils and to compare the growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western red cedar (*Thuja plicata* J. Donn ex D. Donn) seedlings with and without litter. Litter and humus were found to include inoculum of both vesicular–arbuscular (VA) and ectomycorrhizal fungi. Litter amendment usually enhanced growth of host seedlings, but growth enhancement could not be fully attributed to addition of mycorrhizal inoculum or nutrients provided by litter. These findings suggested that other biological factors stimulated the growth of conifer seedlings and (or) activity of mycorrhizal fungi.

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La préparation de stations forestières à la régénération par plantation de conifères comprend souvent le brûlage des rémanents ou la suppression physique de la matière organique du sol. Les auteurs ont exécuté des travaux pour déterminer si la matière organique contribue au potentiel d'inoculum de champignons mycorhiziens dans les sols forestiers et pour comparer la croissance de semis du douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco) et du thuya géant (*Thuja plicata* J. Donn ex D. Donn) avec et sans litière. Des inocula de champignons ectomycorhiziens et endomycorhiziens à vésicules et arbuscules se retrouvent dans la litière et dans l'humus. Des modifications à la litière augmentent généralement la croissance des semis mais l'augmentation de la croissance ne peut être attribuée entièrement à l'addition d'inoculum mycorhizien ou d'éléments nutritifs fournis par la litière. Ces résultats suggèrent que d'autres facteurs biologiques stimulent la croissance de semis de conifères et (ou) l'activité des champignons mycorhiziens.

[Traduit par le journal]

Introduction

Forest regeneration sites are usually cleared and often slash burned before conifer seedlings are outplanted. Particularly adverse sites may sometimes warrant more intensive site preparation, including removal or windrowing of forest floor litter and organic debris ("scalping"), extensive terracing of steep slopes, and mechanical "ripping" to loosen compacted soil in rows where seedlings are to be planted (Stewart 1978). Although the long-term effects of organic matter removal are not known, many foresters reported better initial growth and survival of seedlings planted in mineral soil.

Litter is a substantial source of nutrients in Douglas-fir ecosystems (Youngberg 1966; Fogel and Cromack 1977) and is responsible for up to 72% of aboveground nutrient return in an old-growth stand (Abee and Lavender 1972). Litter and soil organic matter are important in maintaining soil physical properties as well (Kraemer and Hermann 1979). Slash burning can remove up to 75% of soil organic matter (Austin and Baisinger 1955) and leads to nitrogen volatilizaton (Kraemer and Hermann 1979). Resulting ash can cause large increases in available phosphorus, potassium, calcium, and magnesium (Grier and Cole 1971) that are subject to rapid loss by leaching (Grier 1975). Once organic matter is removed, it may take several years to accumulate (Kraemer and Hermann 1979).

Although an apparent allelopathic response of seed-

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ling ectomycorrhizae to forest litter has been reported (Alvarez et al. 1979; Schoenberger and Perry 1982), ectomycorrhizae of older trees develop better in humus and litter layers than in mineral soil (Meyer 1973; Mikola 1973; Harvey et al. 1978; Harvey et al. 1979; Fogel 1980). It is not known if this reflects differences in aeration, moisture relations, pH, availability of nutrients, or activity of microorganisms in the litter layer. Mycorrhizal fungi present in litter layers have been implicated in nutrient cycling, thereby reducing nutrient leaching (Went and Stark 1968; Fogel and Hunt 1979; Fogel 1980). Most of these fungi are considered incapable of saprobic growth and lack enzymes necessary for utilization of complex carbohydrates such as cellulose and lignin (Hacskaylo 1973; Meyer 1974). Ectomycorrhizal fungus-containing litter has been exploited as inoculum for over a century (Trappe 1977) and is probably the most widely used source of ectomycorrhizal inoculum for forest nurseries worldwide (Marx 1980). Advantages of using litter include reliability and relative ease of obtaining large amounts of viable inoculum of fungi presumably adapted to the forest sites from which they were taken; disadvantages include the potential for introducing pathogens into a nursery and the inability to select particular fungus species with specific desirable attributes such as tolerance to drought, high temperatures, or low pH soils (Trappe 1977).

In an earlier study (Parke et al. 1983*a*) fewer ectomycorrhizae were found to develop in soils from old clear-cut and burned areas (average age = 9.4 year) than in soils from undisturbed forests. The present study was undertaken to determine if a loss of organic matter influences mycorrhizal development in soils from disturbed versus undisturbed sites, to determine if forest floor material suppresses growth of conifer seedlings, and to determine if these effects are biological or chemical. To test if forest floor material affects vesicular–arbuscular (VA) and ectomycorrhizal fungi differently, both western red cedar (*Thuja plicata* J. Donn ex D. Donn) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were used in greenhouse bioassays.

Materials and methods

Forest litter and humus were collected in August 1981 from the Boomer Hill study site near Roseburg in southwest Oregon. Located at an elevation of 610 m in the Coast Range north of the Siskiyou Mountains, this area is characterized as a mixed-conifer zone (Franklin and Dyrness 1973) with Douglas-fir (*Pseudotsuga menziesii*) the prevalent tree species. The forest floor consisted of a layer approximately 4 cm deep and included a range of materials from recently fallen needles on the surface to well decomposed humus overlying the mineral soil. Litter and humus were sieved through 0.5-cm mesh to remove large woody material and the mixture was used fresh or pasteurized (65°C for 30 min, aerated steam). An additional control treatment consisted of coarse vermiculite substituted for the litter–humus component. Vermiculite was chosen for its properties of aeration and moisture retention, density similar to litter, and because it is relatively inert, biologically and chemically.

Mineral soil collected from the undisturbed forest and 4-year-old cleared and burned area of the Boomer Hill site was similarly sieved and used fresh or pasteurized (65°C for 30 min, aerated steam). Each of three litter treatments was mixed 1 : 1 (volume basis) with each of four soil treatments to yield a total of 12 soil–litter combinations. These were either sown with surface-sterilized (30% H_2O_2 for 30 min) Douglas-fir seed or planted with 1-month-old western red cedar seedlings in 50 cm^3 tubes (Ray Leach Cone-tainer Nursery, Canby, Oregon, U.S.A.[2]). Each soil–litter treatment per host had 10 replicates.

Seedlings were maintained under greenhouse conditions (24°C day : 18°C night) with a 16-h photoperiod (240 $\mu E\ m^{-2}\ s^{-1}$). All plants were fertilized weekly with 3 mL Long-Ashton nutrient solution (Hewitt 1966) at one-quarter strength phosphorus (11 ppm P).

Douglas-fir seedlings were harvested 16 weeks after germination and their root systems were examined for percent of total feeder root tips which were ectomycorrhizal. Shoot length and shoot and root dry weight were recorded. Western red cedar seedlings were harvested 12 weeks after transplanting. Root systems were excised, chopped into 1-cm segments, bleached in 3% H_2O_2 for 1 h and cleared and stained (Phillips and Hayman 1970). Percent root length colonized by VA fungi was estimated using the technique described by Biermann and Linderman (1981).

Litter and soil components were analyzed for pH, Olsen available phosphorus, and total nitrogen by the Oregon State University Soil Testing Laboratory.

Results

Douglas-fir

Ectomycorrhizae were more abundant on seedlings grown in undisturbed forest soil ($\bar{x}$ = 92.5%) than on seedlings grown in clear-cut soil ($\bar{x}$ = 75.3%), regardless of litter treatment; however, these differences in mean response were not statistically significant ($P < 0.05$) (Table 1). Mycorrhizae did not develop in pasteurized soil treatments unless nonpasteurized litter was added; in these treatments addition of litter restored mycorrhizal colonization to levels comparable to nonpasteurized soils. The addition of litter had no effect on mycorrhiza formation on seedlings grown in nonpasteurized soils. Litter, pasteurized litter, or vermiculite treatments did not differ significantly for these soils.

Shoot height and total weight (Table 1) were greatest

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TABLE 1. Effect of litter on ectomycorrhiza formation and growth of Douglas-fir seedlings

Soil treatment	Amendment		
	Pasteurized litter	Litter	Vermiculite
Undisturbed forest			
% mycorrhizal tips	92*b*	94*b*	92*b*
Shoot height, cm	8.11*a*	11.0*cd*	10.58*bcd*
Total weight, mg	402*bc*	607*e*	538*de*
Undisturbed forest, pasteurized			
% mycorrhizal tips	0*a*	66*b*	0*a*
Shoot height, cm	6.50*a*	11.70*d*	6.80*a*
Total weight, mg	282*a*	552*de*	370*abc*
Clear-cut			
% mycorrhizal tips	79*b*	68*b*	79*b*
Shoot height, cm	7.58*a*	10.16*bc*	6.96*a*
Total weight, mg	340*ab*	506*d*	300*a*
Clear-cut, pasteurized			
% mycorrhizal tips	0*a*	79*b*	0*a*
Shoot height, cm	6.87*a*	9.52*b*	6.64*a*
Total weight, mg	315*ab*	430*c*	348*ab*

NOTE: Values are means of 10 replicates. For each parameter, values not followed by the same letter are significantly different, $P < 0.05$ (Student–Newman–Keuls' test) among the 12 soil × amendment treatments.

for seedlings grown in soils to which litter had been added, and values were larger among undisturbed forest soil treatments than among clear-cut soil treatments. Undisturbed forest soil mixed with vermiculite also yielded seedlings with large shoot height and total weight values, but pasteurized litter and vermiculite did not differ significantly in mycorrhiza colonization, shoot height, or total weight except for the undisturbed forest soil treatment.

Western red cedar

VA mycorrhiza colonization occurred in undisturbed forest and clear-cut soils or in pasteurized soils to which litter had been added (Table 2). Percent root length colonized was slightly higher for seedlings planted in disturbed soil ($\bar{x} = 31.3\%$) compared with seedlings planted in undisturbed soil ($\bar{x} = 26.7\%$) although this difference was not statistically significant ($P < 0.05$). The addition of litter to pasteurized soils restored mycorrhiza colonization to levels comparable to nonpasteurized soil treatments. For nonpasteurized soils, there were no significant differences in VA mycorrhizal colonization between or among litter treatments.

Generally, shoot height and shoot weight were largest for seedlings grown in clear-cut soil regardless of litter treatment and in other soil treatments to which litter had been added. An exception was the undisturbed forest soil + litter treatment, for which shoot weight and shoot height were significantly less than for undisturbed forest soil + pasteurized litter or undisturbed forest soil + vermiculite. Shoot height of mycorrhizal seedlings averaged approximately 94% larger than for nonmycorrhizal seedlings of comparable treatments; shoot weight of mycorrhizal western red cedar seedlings was approximately four times greater than for nonmycorrhizal seedlings.

Glomus tenue (Green) Hall was the only endophyte found in western red cedar roots.

Soil and litter nutrient analyses are summarized in Table 3.

Discussion

Results indicate that litter–humus from the forest floor contains inoculum of both VA and ectomycorrhizal fungi. In contrast to the work by Alvarez et al. (1979) which showed litter to have an apparent allelopathic effect on *Abies concolor* growth and ectomycorrhizae formation, and research by Schoenberger and Perry (1982) on litter and Douglas-fir mycorrhizae, in our study the addition of litter did not affect mycorrhizal colonization of Douglas-fir or western red cedar unless mycorrhizal inoculum was lacking. Compared with treatments including either pasteurized litter or vermiculite, the addition of litter generally enhanced seedling growth of western red cedar and Douglas-fir. The stimulatory effect of litter even when soil inoculum of mycorrhizal fungi was abundant suggests that litter contributes more than added mycorrhizal propagules. When mycorrhizal inoculum was provided in the soil, the difference in growth response between seedlings grown in soil + litter versus soil + pasteurized litter

TABLE 2. Effect of litter on VA mycorrhiza formation and growth of western red cedar seedlings

Soil treatment	Amendment		
	Pasteurized litter	Litter	Vermiculite
Undisturbed forest			
% root length mycorrhizal	25*b*	24*b*	31*b*
Shoot height, cm	4.94*de*	3.94*c*	4.68*d*
Shoot weight, mg	109*c*	67*b*	103*c*
Undisturbed forest, pasteurized			
% root length mycorrhizal	0*a*	31*b*	0*a*
Shoot height, cm	3.15*bc*	5.19*de*	2.50*ab*
Shoot weight, mg	49*ab*	112*c*	20*a*
Disturbed			
% root length mycorrhizal	30*b*	33*b*	31*b*
Shoot height, cm	5.29*de*	5.32*de*	5.81*e*
Shoot weight, mg	135*ce*	159*d*	154*d*
Disturbed, pasteurized			
% root length mycorrhizal	0*a*	30*b*	0*a*
Shoot height, cm	3.38*c*	5.27*de*	2.11*a*
Shoot weight, mg	38*ab*	120*c*	16*a*

NOTE: Values are means of 10 replicates for each parameter. Values not followed by the same letter are significantly different, $P < 0.05$ (Student–Newman–Keuls' test) among the 12 soil × amendment treatments.

TABLE 3. Nutrient analysis of soil-amendment combinations

Soil + amendment	pH	P (ppm)	Total N (%)
Undisturbed forest			
+ pasteurized litter	6.8	26	0.32
+ litter	6.8	23	0.33
+ vermiculite	6.9	20	0.24
Undisturbed forest, pasteurized			
+ pasteurized litter	6.9	28	0.31
+ litter	6.8	25	0.32
+ vermiculite	7.0	22	0.23
Clear-cut			
+ pasteurized litter	6.3	23	0.25
+ litter	6.3	21	0.26
+ vermiculite	6.5	18	0.17
Clear-cut, pasteurized			
+ pasteurized litter	6.3	23	0.25
+ litter	6.3	21	0.26
+ vermiculite	6.5	18	0.17

indicates further that it is a biological rather than nutritional effect; litter may contain microorganisms stimulatory to seedling growth or mycorrhizal fungus metabolic activity and nutrient uptake (Meyer 1974; Bowen and Theodorou 1979).

Another possible explanation for growth differences is that pasteurization of litter results in formation or release of compounds deleterious to plant growth and (or) mycorrhizal fungus activity. It is unlikely that this would have occurred at the temperature and duration of pasteurization used (65°C for 30 min). The addition of pasteurized litter and, to a lesser extent, the pasteurization of undisturbed forest soil resulted in insignificant increases in phosphorus availability (Table 3). It is doubtful that these increases could have resulted in P levels inhibitory to mycorrhizal colonization since mycorrhizal dependency experiments (J. Parke, unpublished) suggest that mycorrhizal colonization is not impeded by fertilization with 43 ppm P nutrient solution.

Peuss (1958) observed that addition of peat to soil reduced colonization and growth enhancement by VA mycorrhizal fungi. Biermann (1982) found that peat decreased the growth response of mycorrhizal plants only when the planting medium lacked soil; solution P increased to a high level if not removed from solution by soil. Thus, the apparent inhibition of mycorrhizal fungi by organic matter (and other soilless media) was actually a phosphorus effect.

In contrast with an earlier study (Parke et al. 1983*a*), the inoculum potential of mycorrhizal fungi in soil from the clear-cut in this experiment was not significantly different from undisturbed forest soil. One reason for this might be the difference in time since disturbance for the clear-cuts: 9.4 years for the earlier study vs. 4 years for this experiment. Further investigations on young (1.5-year-old) clear-cuts confirmed that the inoculum potential of recently disturbed sites is not significantly less than undisturbed sites (Parke et al. 1983*b*).

Mycorrhizal fungi are generally considered to be

parasites that are unable to complete their life cycles in the absence of a suitable living host, and many have little or no growth potential on nonliving substrates. The ability of ectomycorrhizal fungi to utilize complex carbohydrates in axenic culture is restricted to a few genera (Meyer 1973, 1974; Hacskaylo 1973), although ectomycorrhizal fungi isolated from rotten wood have formed ectomycorrhizae with conifer hosts in pure culture and in the field (Kropp 1982), and decayed wood and humus can be the major substrates for ectomycorrhizal fungi (Harvey et al. 1978; Harvey et al. 1979). VA mycorrhizal fungi have been shown to colonize senescent roots of nonhost plants (Hirrel et al. 1978; Parke and Linderman 1980; Ocampo and Hayman 1981) and to spread independently through soil in the absence of host roots (Warner and Mosse 1980). *Glomus tenue* has been found in association with bryophytes distant from soil or roots of higher plants (Johnson 1977). The potential for mild saprobism by VA mycorrhizal fungi in general, and *Glomus tenue* in particular, should be further investigated. Even if active saprobism does not occur, it is quite possible that mycelium or spores of mycorrhizal fungi associated with plant roots in the litter layer may survive as dormant propagules in this substrate.

Mycorrhizal fungi have been identified as important components in nutrient cycling in Douglas-fir ecosystems (Fogel and Hunt 1979; Fogel 1980). In the absence of a litter layer and fungi to mobilize and transfer these nutrients to plant roots, nutrients may be leached deep in the soil, thus becoming unavailable to young outplanted conifer seedlings. Loss of this organic matter through burning or scalping may result in initial decreases in mycorrhizal inoculum, loss of microorganisms stimulatory to seedling growth and (or) mycorrhizal activity, and with time, decreased availability of nutrients to growing seedlings.

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